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Nutrient Effect on Fall Leaf Abscission in Northern Hardwood Forests

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Abstract

Excess nutrients in ecosystems may be altering deciduous tree phenological events. By having delayed autumn leaf abscission, the length of the growing season may be extended, which could increase forest productivity. Nitrogen (N) availability due to nitrogen deposition from anthropogenic pollution, in turn making phosphorus (P) limitation more likely. This study examines the effect of nitrogen and phosphorus additions on leaf retention at a community-level in hardwood forests and a species-level (American beech, sugar maple, red maple, paper birch, yellow birch, and pin cherry) located in 12 stands of different ages located in New Hampshire, USA. These stands were part of Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE), which contains plots that are either unfertilized or treated with N, P, or both N + P. Multiple leaf litter collections occurred four times in the fall of 2016 and once more in June of 2017. At a community-level, P-fertilized trees increased leaf retention by 16% (p = 0.01). Some species also experienced increased leaf retention due to P-additions: yellow birch trees increased leaf retention by 58% (p = 0.05) and pin cherry trees retained 24% more leaves (p = 0.05). N fertilization also increased leaf retention by 7% at community-level (p = 0.04), but promoted early leaf drop in American beech trees by 3% (p = 0.04). Both N and P fertilization caused sugar maple to retain less leaves than when fertilized by a single nutrient. Conversely, red maple trees fertilized with both N and P retained more leaves than a single nutrient addition. Increased nutrient availability from fertilization reduces the need for the trees to resorbed the foliar nutrients, as well as availability leads to longer leaf retention which may increase the length of the growing season and the total gain of carbon. This will have an impact on any forests experiencing nutrient influxes, which could alter their productivity.

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Glossary of Terms

Leaf life-span – The time between bud burst and leaf abscission.

Marcescence – The

Retention – The time leaves are retained in the canopy in autumn.

Senescence – The onset of leaf coloration to

Introduction

The timing of plant phenological events are defined the growing season, especially in deciduous hardwoods. A longer growing season is accomplished by early budburst and/or delayed leaf senescence (Estiarte & Penuelas, 2015). The onset of autumn senescence and the timing of leaf fall defines the end of seasonal productivity. The process of deciduous leaf senescence is the degradation of chlorophyll, the resorption of foliar nutrients, and the abscission of leaves. Altering fall phenology of deciduous trees can modify forest community productivity (Estiarte & Penuelas, 2015).

The end of the forest growing season is measured by the timing of abscission or senescence. Leaf senescence is initiated by many variables which include the length of photoperiod (Estiarte & Penuelas, 2015), ambient temperatures (Doi & Takahashi, 2008), and less importantly, moisture availability (Williams *et al*., 1997). Another abiotic factor in determining leaf lifespan is nutrient status. In environments with poor nutrient availability, an adaptation to conserve nutrients and promote nutrient use efficiency is to increase leaf retention (Escudero et al., 1992). Here, we measured the timing of leaf abscission since leaf abscission and leaf senescence are normally linked (Killingbeck, 2004).

Nutrient status can have an effect on the timing of leaf abscission (Escudero et al., 1992). Due to anthropogenic activity since the industrial revolution, nitrogen (N) deposition has increased N availability in northeastern United States (Aber *et al.,* 2003). The addition of N has yielded contradicting effects on leaf life-span. A review of N showed under low N availability, leaf lifespan is shortened by early abscission, but leaf retention is promoted when N is readily available that the strength of the internal N sink is minimized (Pornon *et al*., 2011). The paradox of nitrogen effects on leaf retention opens questions on how leaf lifespan is affected by the

addition of the most limiting nutrient to a system. An increase in N availability in northeastern forests have shifted the limiting nutrient from N to phosphorus (P) in some areas (Gradowski & Thomas, 2006 and Vadeboncoeur *et al.,* 2014). To our knowledge, there is no study examining the effects of P on autumn leaf retention in hardwood forests.

Populations within hardwood communities can be examined for leaf retention. Besides timing of leaf fall, there is variation in forest community leaf drop due to differences among species (Niinemets amd Tamm, 2005). Species have unique life strategies and nutrient use efficiencies which add disparity of leaf drop in mixed-species communities. Northern hardwood forests are dominated by various species of maple (*Acer*) and birch (*Betula*) as well as American beech (*Fagus grandifolia*) trees. Species show variations in leaf drop (Richardson *et al.,* 2006). For instance, American beech is a marcescent species which retains its foliage into winter long after autumn leaf fall other deciduous species.

The aim of this study is to investigate the effects of N and P additions on autumn leaf retention in northern hardwood forest communities and species within these stands. In the White Mountains of New Hampshire, there are established stands with plots that have been fertilized for six years with N and P. The growth of the trees in these study sites are limited by P (Goswami *et. al.,* 2018). Our main objectives are to test the effect of N and P fertilization on (1) leaf abscission in hardwood forests on a community-level, (2) the response of leaf retention in different forest age classes, and (3) the timing of leaf fall in various hardwood species.

Methods

Site Description

This research was conducted at three sites in the White Mountains of New Hampshire, USA: Bartlett Experimental Forest (BEF), Hubbard Brook Experimental Forest (HB), and Jeffers Brook (JB) (Fig. 1). These sites share similar glacial drift established Spodosol soils and a humid

continental climate. Stands varied in age from 28 to 137 years and are categorized into three age classes: young (clearcut 1985-1990), mid-age (clearcut 1975-1978), and old (1883-1890) (Table 1). Stands contain plots fertilized in a 2 x 2 factorial design (control, N, P, and N + P) as part of a larger study, Multiple Element Limitation on Northern Hardwood Ecosystems (MELNHE; http://www.esf.edu/melnhe/default.htm). Each plot is 30 m x 30 m and is surrounded by a 10 m buffer, except for the mid-age stands in JB and HB which contain plots that are 20 m x 20 m with 5 m buffers. BEF stands were coded with C numbers (C1, C2, C4, C5, C6, C7, C8, C9) with young, mid-aged, and mature stands, whereas HB and JB are only differentiated between middle-aged (-M) and mature (-O) stands (HBM, HBO, JBM, JBO) (Table 1). Since 2011, these plots have been fertilized annually with N (NH_4NO_3) at the rate of 30 kg N $ha^{-1}yr^{-1}$ and P (NaH_2PO_4) at the rate of 10 kg P $ha^{-1}yr^{-1}$.

Due to succession, stands of different ages contain distinctive tree species. Mature-stand trees are mainly composed of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). The dominant trees in young stands are American beech, yellow birch, white birch (*Betula papyrifera*), red maple (*Acer rubrum*) and pin cherry (*Prunus pensylvanica*). Mid-aged stands contain all of these species, with a reduced abundance of pin cherry.

Leaf Litter Collection

In August of 2016, 20 collection baskets with a surface area of 0.234 m^2 were placed in each of the 12 stands. Five baskets were positioned in each of the four plots. The plots of BEF were divided into nine 10 m x 10 m subplots and JBM and HBM were divided into four 10 m x 10 m subplots. The baskets were set in the middle of five of the nine subplots (one in the center subplot and one in each corner subplot). The baskets had vented sides, bottom drainage holes, and open tops.

Litter collection took place over five dates between October 2016 and June 2017. The first collection occurred during the peak of autumn color (October 7th- 8th). Two weeks later, between October 17th – 19th, the second collection took place. Collection date three occurred between October 22nd – 24th. Then the final autumn collection occurred once most trees were defoliated, between November 2nd– 6th. An additional collection was completed during June 1st – 4th, 2017 to collect any final leaves that fell after Nov. 5th. The spring collection was used to investigate nutrient effects of American beech leaf abscission because they exhibit marcescence. Dry litter was collected and stored in paper bags, whereas wet litter was collected in plastic bags and stored on ice. To prevent decomposition, all litter was frozen until processing. If a collection basket was damaged or altered in a way that interfered with litter accumulation, the litter was removed from this study. Stands C7, HBM, and HBO were not collected for Oct. 7th -Oct. 8th and JBM, JBO, HBM, and HBO were not collected on Oct. 22nd-24th.

Leaf Litter Processing

Leaf litter collected from stands C4, C5, C7, C8, HB, and JB were oven-dried at 60 ºC and weighed to the nearest centigram. Litter from stands C1, C2, C6, and C9 were sorted by species before they were oven-dried and weighed.

Data Analysis

For community-level analysis, the litter mass from the five baskets in each treatment plot was averaged to represent the treatment. Treatment plot was the unit of replication. This averaged mass at each collection date was divided by the total mass of litter in the plot to describe the litterfall as a percentage of the total. Separate analyses were used at each collection date. The first analysis included the percentage of litter that had fallen from August to Oct. 7th - 8th (n = 44, n = 11 per treatment). The second analysis uses the percentage of litter fallen from August to Oct. 17th – 19th (n = 48, n = 12 per treatment). The third and forth analyses follow the

same pattern in which the percentage of litter fallen from August to Oct 22nd – 24th (n = 40, n = 10 per treatment) and Nov. 2nd – 6th (n = 48, n = 12 per treatment). The percentage of leaf retention was the inverse of the percentage of fallen litter.

To test for treatment effects on leaf retention at a community level, we used a mixed-effects model (Proc Mixed, SAS Studio 3.71, Cary, NC, USA) with treatments (N or P additions) and stand age as fixed effects and site and stand (nested in site) as random effects. The factorial design compares plots fertilized with a treatment to those without that treatment (N addition = N and N+P plots compared to control and P plots; P addition = P and N+P plots compared to control and N plots). We also test the interactions between N and P additions. A post-hoc Tukey comparisons of least-squares means was used to examine the effects of N+P interactions or N or P additions. P values were considered significant if < 0.05.

To investigate nutrient effects at a species level, a species leaf litter had to contribute at least 1% of the total mass of each plot in a stand (minimum of 3 g; approximate mass of a leaf = ~ 0.1 g) for it to contribute to our analysis. Therefore, the sample sizes depended on which species litter was frequent enough to represent leaf retention; American beech (stands C1, C2, C6, and C9; n = 16), red maple (C1, C2, and C6; n = 12), sugar maple (C6 and C9; n = 8), white birch (C1, C2, and C6; n = 12), yellow birch (C1, C2, C6, and C9; n = 8), and pin cherry (C1 and C2; n = 8) (Table 2).

Using the same methods as in the community-level data, the mass of a species in the five baskets was averaged in each plot. First, percentage of the mass of fallen litter was calculated for each collection period. Then the inverse was taken to describe the percentage of leaves retained in the canopy.

Since not all species were represented in all stands, we ran a separate model for each species to test for treatment effects on leaf retention. We used a mixed-effects model with treatments (N and P additions) and stand as fixed effects. This model was similar to the community-level model and was examined the same.

Separate analyses of variance tested for significant differences in leaf retention of trees in each treatment plots (control, N, P, and NP).

Results

Community-level

P and N fertilization effects on leaf retention

Trees fertilized with P retained more leaves at the beginning of autumn than trees not fertilized with P. Trees in P-treated plots retained 2.5% more leaves ($p = 0.04$) on Oct. 7^{th} - 8^{th} and 16% ($p < 0.01$; fig. 2) on Oct. 17^{th} - 19^{th}. There was no significant difference in leaf retention for P-fertilized trees on Oct. 22^{nd}-24^{th} and Nov. 2^{nd} - 6^{th}.

N fertilization also delayed leaf abscission. On Oct. 17^{th}-19^{th}, N-fertilized trees retained 7% more leaves than non-N-fertilized trees ($p = 0.04$), whereas no effects were observed at any other collection date.

There was no significant interaction of N and P on leaf retention. However, on Oct. 17^{th} - 19^{th}, trees in N+P plots retained 23% more leaves than unfertilized trees in the control plots ($p = 0.01$).

Stand age effects on leaf retention

The timing of leaf fall was different among age classes of stands. On Oct. 17^{th}-19^{th}, trees in young stands dropped 40% more leaf litter than old stands ($p = 0.01$). No other dates showed a detectable difference in percentage of leaves retained. There were no significant interactions of age and treatment.

Species-level

P fertilization effects on leaf retention in species

Phosphorus fertilization increased autumn leaf retention in four of six hardwood species (fig. 3). On Oct. 7^{th} - 8^{th}, pin cherry trees fertilized with P retained 24% more leaves than those not fertilized with P ($p = 0.05$; fig. 2a). On Oct. 17^{th}-19^{th}, P-fertilized yellow birch trees retained 58% more litter than yellow birch trees without P fertilization ($p = 0.05$; fig. 3b).

N fertilization effects on leaf retention in species

N fertilization promoted early leaf abscission in American beech trees. On Oct.7^{th} - 8^{th}, American beech trees fertilized with N abscised 3% more leaves than American beech trees not fertilized with N ($p = 0.04$; fig. 3f).

N and P interactions on leaf retention

Maple trees were very responsive to N and P fertilizations. Sugar maple trees fertilized with both N and P retained 45% more leaves than the control sugar maple trees ($p < 0.01$; fig. 2d). When fertilized with only a single nutrient, sugar maple leaf retention increased. Sugar maple trees that have been fertilized with P alone increased their leaf retention by 69% compared to the control trees ($p = 0.01$). Sugar maples fertilized with only N retained 59% more leaves than control sugar maple trees ($p = 0.03$).

Red maple trees also had an interaction with both N and P fertilizations (fig. 3e). When fertilized with both N+P, red maple trees retained 62% more leaves than the unfertilized control red maple trees ($p = 0.02$). However, when red maple trees were fertilized with either N or P, leaf retention was not significantly different from the control (P additions $p = 0.07$; N additions $p = 0.08$); the average leaf retentions with the nutrient additions were observably lower than the average of the control tree leaf retention (P plot trees retained 33% fewer leaves; N plot trees retained 27% less leaves).

Stand differences

The leaf retention of some species behaved significantly different among stands. On Oct. 7th - 8th, yellow birch trees in C1 (young stand) dropped 26% more leaves than C6 (mid-age) yellow birch trees (adjusted $p = 0.04$) and 31% more leaves than C9 (old) trees (adjusted $p = 0.01$; $p = 0.01$). On Oct. 17th-19th, yellow birch trees in C1 dropped 73% more leaves than C9 (adjusted $p = p < 0.01$). C2 (young) yellow birch trees dropped 71% more leaves than yellow birch trees in C6 (adjusted $p = 0.04$), and 78% more leaves than trees in C9 (adjusted $p < 0.01$; $p < 0.01$; fig. 3b).

On Oct 17th-19th, white birch trees in C1 dropped 50% more leaves than C6 (adjusted $p < 0.01$) and C2 dropped 51% more than C6 (adjusted $p < 0.01$; $p < 0.01$). On Oct 22nd-24th, C1 white birch trees dropped 169% more leaves than C2 trees (adjusted $p = 0.02$) and 125% more leaves than C6 trees (adjusted $p = 0.03$; $p = 0.01$; fig. 3c).

On Oct. 17th-19th, red maple trees in C1 dropped 72% more leaves than C6 trees (adjusted $p < 0.01$) and C2 trees dropped 68% more leaves than C6 trees (adjusted $p < 0.01$, $p < 0.01$; fig. 3e).

Sugar maple trees in C6 on Oct. 17th-19th retained 32% more leaves than C9 trees ($p < 0.01$; fig. 3d).

Pin cherry trees in C2 on Oct. 8th dropped 28% more leaves than C2 pin cherry trees ($p = 0.02$). On Oct. 17th-19th, pin cherry trees in C2 dropped 54% more leaves than C1 trees ($p = 0.03$; fig. 3a).

Discussion

Our forest stands retained their leaves longer with P fertilization at community- and species-levels. This result is particularly interesting because P fertilization effects on leaf

retention have yet to be investigated in hardwood. Due to anthropogenic pollution, hardwoods could have a longer growing season. Both N and P are mobile elements and are withdrawn from senescent leaves (Estiarte & Penuelas, 2015) and their resorption efficiencies are similar (Vergutz *et al*. 2012). It may be possible that the effects of P availability mimic the effects of N availability on leaf retention. When P is the most limiting nutrient and is added to the system, leaf abscission is delayed because the strength of the endogenous P sink is minimized. The need for the tree to allocate P elsewhere in the tree is insignificant and leaves are maintained. When there is no strong sink influence, leaf abscission occurs when the net carbon gain of the leaf is reduced to zero (Anten & Poorter, 2009).

At a community-level, N fertilization also increased leaf retention, but to a lesser magnitude than P additions. Unsurprisingly, the trees in our stands are less dependent on exogenous N than they are by P. However, N additions promoted early leaf abscission in American beech trees. This contradiction may be due to species specific nutrient allocation and life strategy (Escudero *et al.,* 1992). American beech is the only leaf litter sorted from a marcescent species in this study. Marcescent species have been thought to retain their leaves to maximize their nutrient use efficiencies. Under fertilization, American beech trees may be satisfied by the N available from the soil, so they drop their leaves earlier in the season. Nonetheless, these results contribute to the inconsistencies detected in leaf lifespan from N availability.

Both sugar and red maple trees showed significant interactions with N and P fertilizations. These results are particularly interesting because these maple species demonstrate different interactions to the fertilizers. Sugar maples exhibited increased leaf retention when trees were fertilized with N and P separately, but when combined, the increased leaf retention was

reduced. However, red maple trees increased leaf retention with the addition of both N and P, but not when a single nutrient was added. A possible explanation of variation between species is due to species-specific nutrient requirements and nutrient use efficiencies. Sugar maple leaves are rich in N (Lovett *et al*., 2004) and red maple leaves tend to have low foliar N levels compared to other species (Abrams, 1998). When both nutrients are combined in sugar maple, an imbalance between the limiting nutrients may reduce leaf retention in sugar maple. While red maple may be limited by N and P at a balanced level, so when the treatments are combined, leaf retention increases.

Autumn leaf retention within community- and species-levels were significantly different among age classes. At a community level, trees in young stands dropped their foliage earlier than trees in old stands. For the most part, individual trees in different species followed a similar pattern in that trees within a species dropped their leaves in younger stands sooner than trees in older stands. Species-level observations must be interpreted with care due species having few replicates in stand age classes. The variation among trees in different stand ages may be due to differing life stages. Mature trees have an increased basal area and therefore are able to hold larger internal pools of nutrients (Chapin *et al.,* 1986). Fewer stored nutrients may cause younger trees to be more dependent on nutrient resorption from the leaves. Therefore, the internal nutrient sink is stronger and leaves are abscised sooner.

Conclusion

The timing of leaf abscission affects productivity. Delayed leaf senescence extends the growing season (Dragoni *et al.,* 2011) which may increase carbon sequestration (Estiarte & Penuelas, 2015). Individuals that are able to sequester carbon late in the season may have a

competitive advantage over those that drop their leaves early in autumn. This may lead to an eventual shift in species composition. However, the trade-off of delayed leaf abscission is an increased risk of frost damage which may lead to incomplete senescence (Estiarte & Penuelas, 2015). Unfinished nutrient resorption from senescing leaves may outweigh the benefits of carbon-gain from late leaf fall.

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Tables and Figures

Table 1. Site description of stands in Bartlett Experimental Forest (BEF), Hubbard Brook Experimental Forest (HB), and Jeffers Brook Forest (JB), NH, USA. Species codes are ACRU (*Acer rubrum*), ACSA (*Acer saccharum*), BEAL (*Betula alleghaniensis*), BEPA (*Betula papyrifera*), FAGR (*Fagus grandifolia*), and PRPE (*Prunus pensylvanica*).

Stand	Site	Year Cut	(age class)	Lat.	Lon.	Elevation (MASL)	Aspect	Slope (%)	Dominant Species
C1*	BEF	1990	(young)	44º 02′N	71° 19′W	570	SE	5-20	PRPE, BEPA, FAGR, ACRU
C2*	BEF	1988	(young)	44° 04′N	71° 16′W	340	NE	15-30	BEPA, ACRU, FAGR, PRPE
C3	BEF	1980	(young)	44° 02′N	71° 18′W	590	NNE	8-20	BEPA, ACRU, FAGR, ACSA, PRPE
C4	BEF	1978	(mid-age)	44º 03′N	71° 16′W	410	NE	20-25	PRPE, ACRU, BEPA
C5	BEF	1976	(mid-age)	44º 02′N	71° 19′W	550	NW	20-30	BEPA, ACRU, PRPE, FAGR
C6*	BEF	1975	(mid-age)	44° 02′N	71° 16′W	460	NNW	13-20	BEPA, ACRU, FAGR, PRPE, BEAL
C7	BEF	~1890	(mature)	44º 03′N	71° 18′W	440	ENE	5-10	FAGR, ACSA, BEAL
C8	BEF	1883	(mature)	44° 03′N	71° 18′W	330	NE	5-35	BEAL, ACSA, FAGR
C9*	BEF	~1890	(mature)	44° 03′N	71° 17′W	440	NE	10-35	BEAL, ACSA, FAGR
HBM	HB	1971	(mid-age)	43º 56′N	71° 44′W	500	S	10-25	BEAL, PRPE, BEPA, ACRU
HBO	HB	~1910	(mature)	43º 56′N	71° 44′W	500	S	25-35	FAGR, BEAL, ACSA
JBM	JB	1985	(mid-age)	44º 02′N	71° 53′W	730	WNW	25-35	PRPE, ACSA, BEAL, BEPA
JBO	JB	~1900	(mature)	44º 02′N	71° 53′W	730	WNW	30-40	ACSA, BEAL, FAGR

*Litter was sorted by species

Table 2. 'X' represents prevalent species (mass > 1%) from litter in each plot for analyzing species in the stand for each treatment. Species codes are FAGR (*Fagus grandifolia*), BEAL (*Betula alleghaniensis*), BEPA (*Betula papyrifera*), ACRU (*Acer rubrum*), ACSA (*Acer saccharum*), and PRPE (*Prunus pensylvanica*).

Stand	FAGR	BEAL	BEPA	ACRU	ACSA	PRPE
C1	X	X	X	X		X
C2	X	X	X	X		X
C6	X	X	X	X	X	
C9	X	X			X	

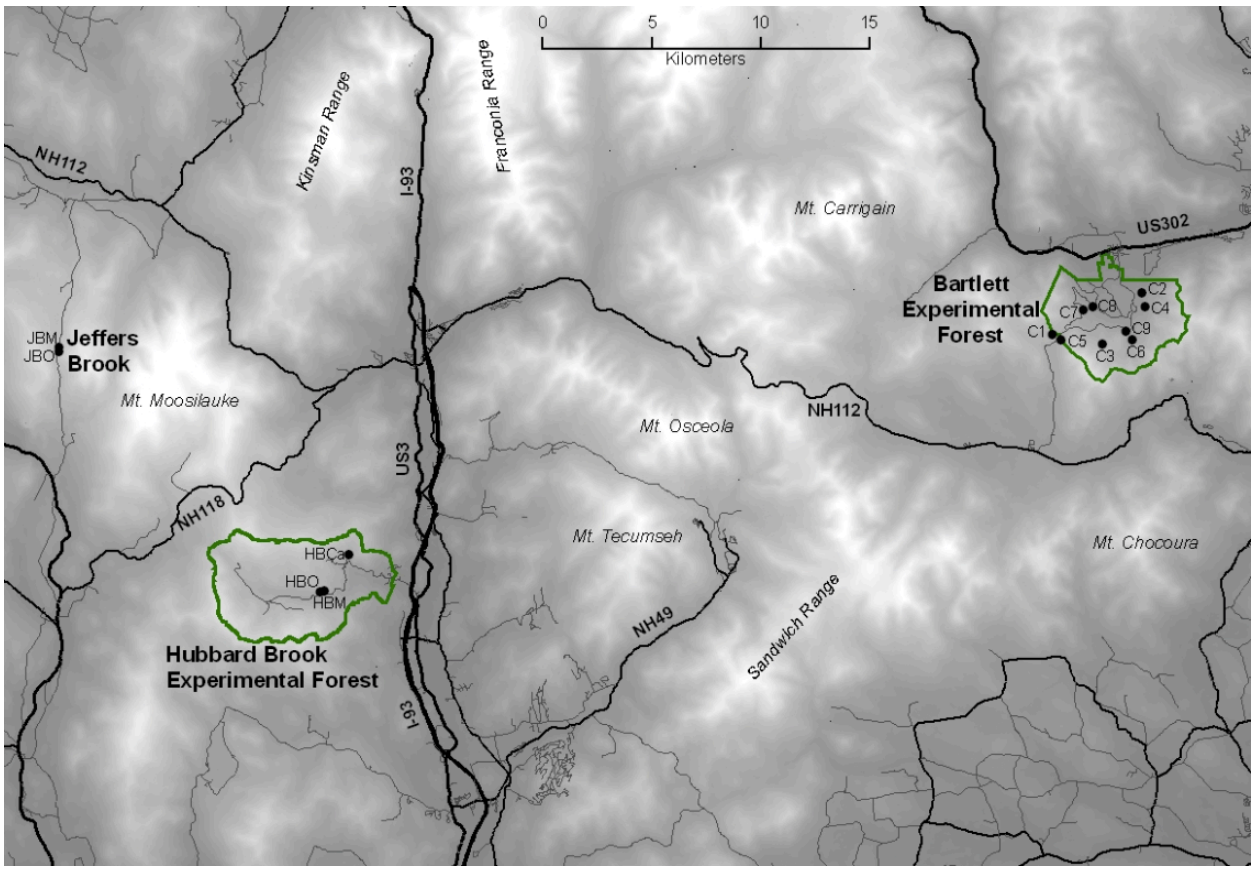

Figure 1. The location of Bartlett Experimental forest (C), Jeffers Brook Forest (JB) and Hubbard Brook Experimental Forest (HB), NH, USA.

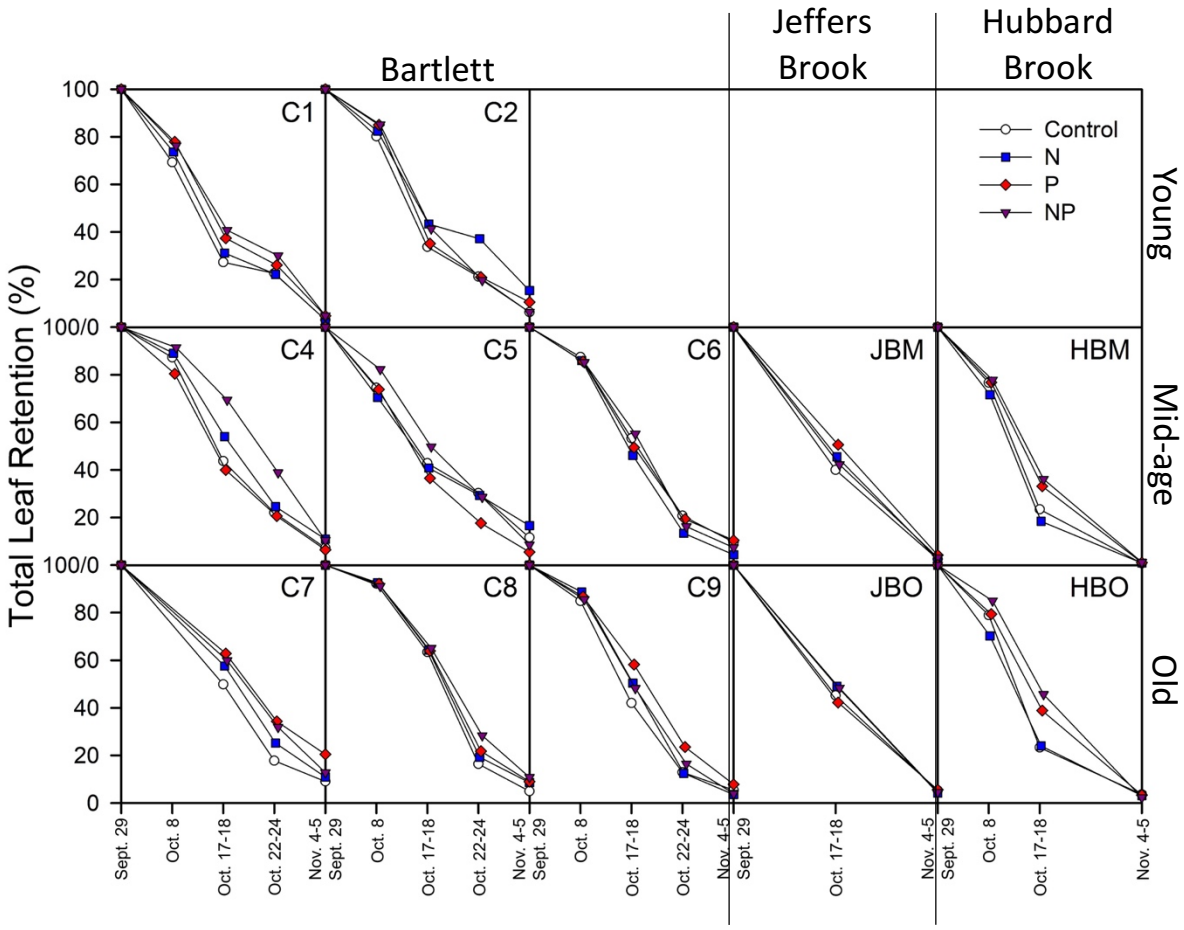

Figure 2. The average proportion of leaves retained in autumn of 2016 in treatment plots (n=5) in each stand from Bartlett Experimental forest (C), Jeffers Brook Forest (JB) and Hubbard Brook Experimental Forest (HB), NH, USA. Collection baskets amassed litter from August 2016 to June 2017. A fourth/fifth collection panel is not shown because all leaves have fallen at that time (leaves retained in canopy = 0%). Richardson et al.'s (2006) model determined September 29th was the start of senescence and phenocameras in Hubbard Brook and Bartlett verified this date (https://phenocam.sr.unh.edu/webcam).

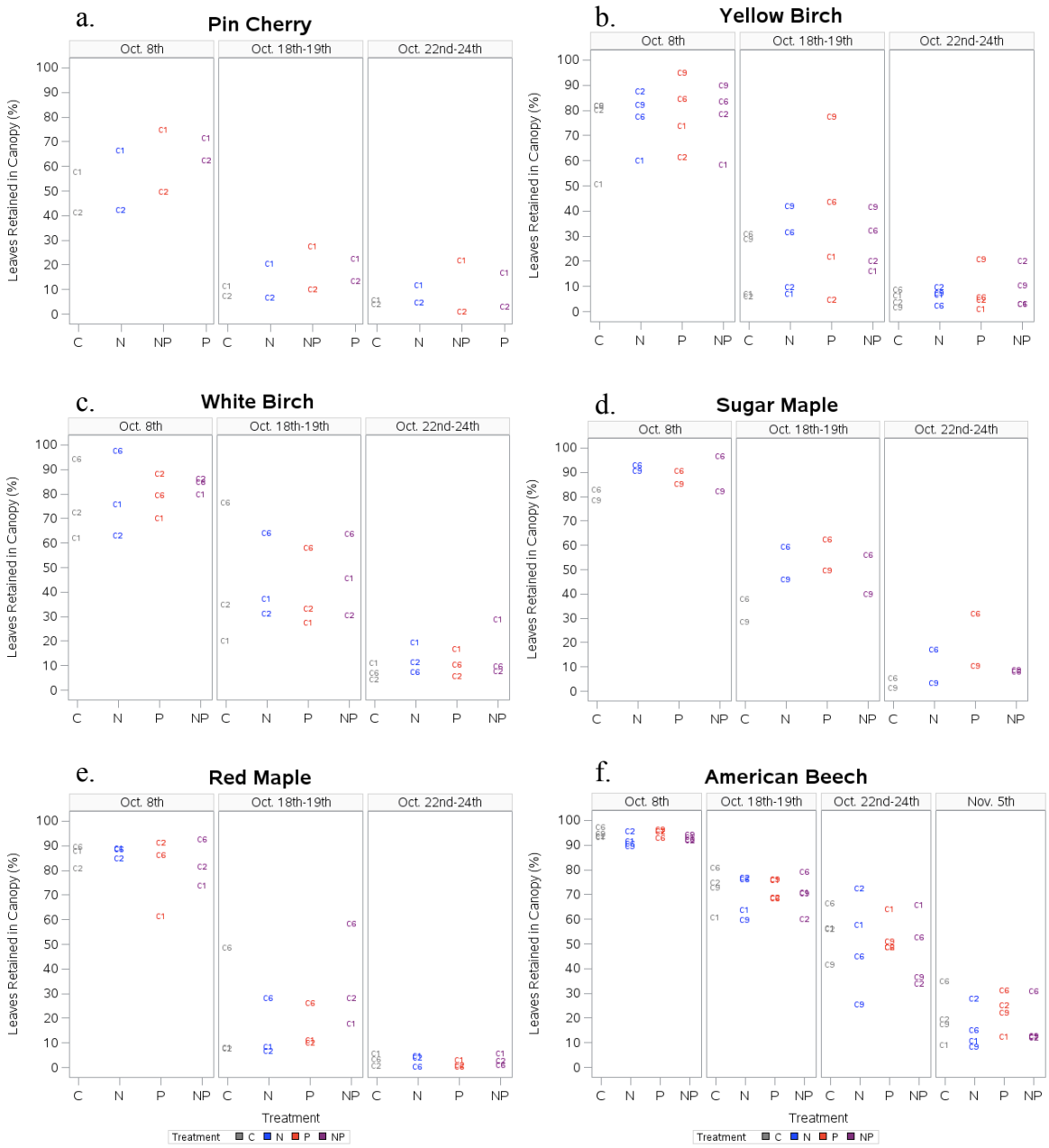

Figure 3. The percentage of leaves retained for (a.) pin cherry (n = 8), (b.) yellow birch (n = 16), (c.) white birch (n = 12), (d.) sugar maple (n = 8), (e.) red maple (n =12), and (f.) American beech (n= 16) in each treatment plot at the collection dates. Collection baskets amassed litter from August 2016 to June 2017. Litter was collected and sorted four times in autumn and once more for American beech in June 2017. A fourth/fifth collection panel is not shown because all leaves have fallen at that time (leaves retained in canopy = 0%).